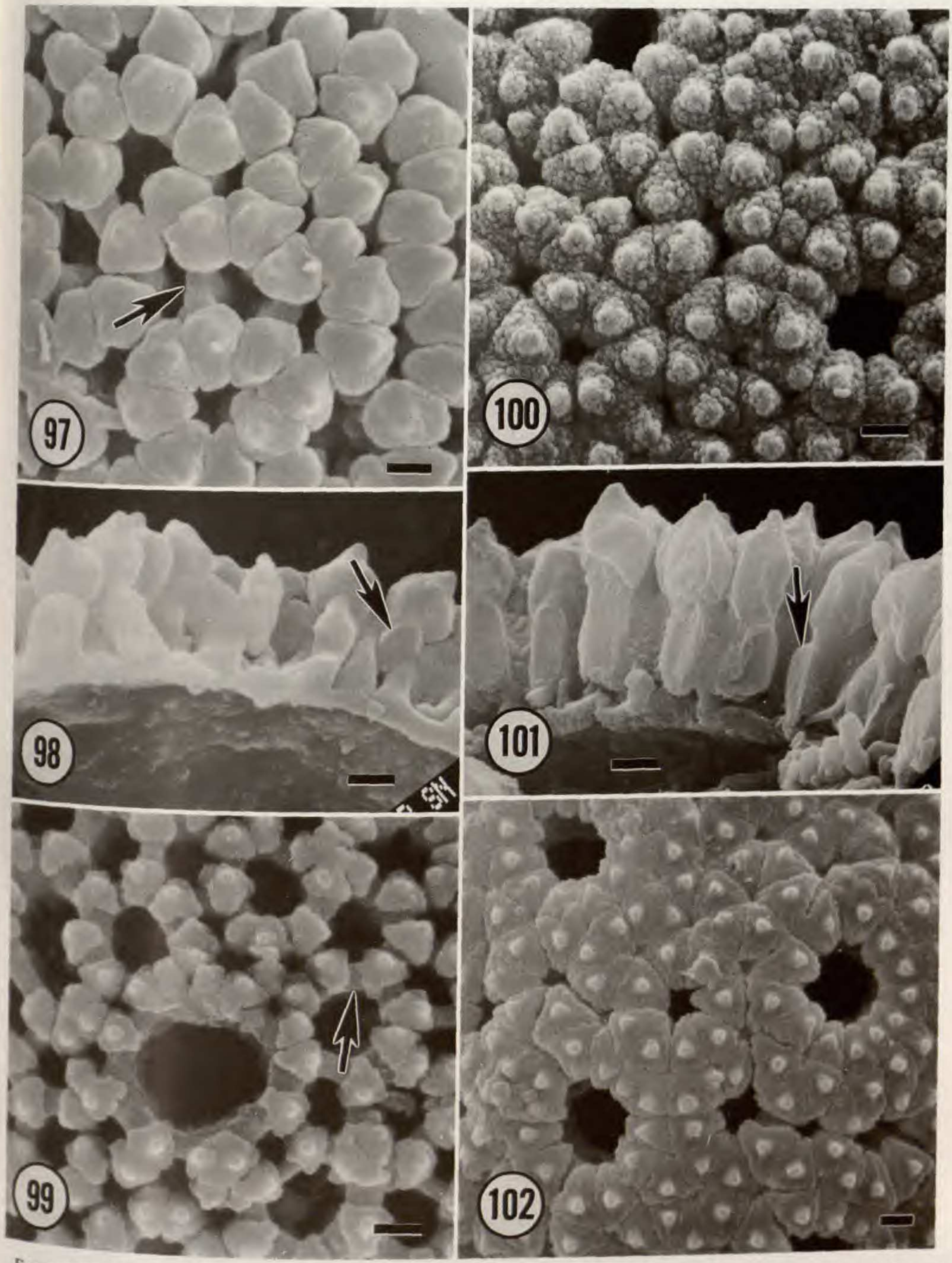


FIGURES 97–102.[3] SEM of pollen of Thymelaeaceae. 97, 98. *Gyrinopsis cumingiana*.—97. Tectum. Arrow marks muri.—98. Fracture. Arrow marks broken muri.—99. *Schoenobiblus grandifolia*. Tectum including pore.—100. *Pimelea prostrata*. The close spacing of subunits obscures muri.—101. *Gnidia glauca*. Fracture illustrating broken edges (arrow) of vertically elongated muri.—102. *Pimelea ligustrina*. Tectum.

LATICIFERS IN CROTONOIDEAE (EUPHORBIACEAE): HOMOLOGY AND EVOLUTION[1]

Paula Rudall[2]

ABSTRACT

Laticifer distribution is described in several genera of Euphorbiaceae, particularly in subfamily Crotonoideae, previously neglected in this respect. Branched, nonarticulated laticifers are common in both Crotonoideae and Euphorbioideae, sparse in Acalyphoideae (occurring in, e.g., *Omphalea*), and absent in the other two subfamilies. However, many genera without latex have elongated, highly branched sclereids in the mesophyll, which may in some instances be homologous with laticifers. Typical articulated laticifers (consisting of numerous fused cells) are currently known in only three genera of Crotonoideae, although several anomalous and transitional forms are reported. Crotonoideae differs from Euphorbioideae in that nonarticulated laticifers originate in the protophloem, and are in general more abundant in the phloem, in common with articulated laticifers. Laticifer evolution is discussed in relation to the phylogeny of Euphorbiaceae.

The objectives of this investigation are to assess the phylogenetic significance of laticifers in Euphorbiaceae with particular reference to the subfamily Crotonoideae and to a lesser extent Acalyphoideae, both less well known than Euphorbioideae in this respect (Rudall, 1987). Ontogenetic data are important in this type of investigation, but are limited by the availability of sufficient material. The role of ontogenetic data in systematics has seen a recent resurgence of interest, especially with respect to the establishment of homologies of features present at maturity. This aspect has particular relevance to a study of laticifers, where development is important in the classification of the different types. Most recent investigations of laticifer development in Euphorbiaceae have concentrated on *Euphorbia* and closely related genera in Euphorbioideae (e.g., Mahlberg & Sabharwal, 1968). Developmental studies on other genera are scanty, largely owing to the difficulty of obtaining suitable material. Those that do exist (e.g., Chauveaud, 1891; Gaucher, 1902) need updating in the light of modern methods and taxonomic concepts. Chauveaud (1891) examined several genera of Euphorbioideae and three species of Crotonoideae, *Aleurites triloba*, *Croton pungens*, and *Jatropha curcas*, but without illustrations. Scott (1884a, b, 1886) examined articulated laticifers in embryos of *Manihot* and *Hevea*, both Crotonoideae.

Webster (1975) used latex production and presence or absence of laticifers as characters in his classification of Euphorbiaceae into five subfamilies; however, information on both is frequently lacking in the literature. Records of latex exudation indicate the presence of laticifers, but lack of such records may simply mean that the latex, if present, is not conspicuous. Latex is of very widespread occurrence among Crotonoideae and Euphorbioideae, but varies in color and abundance. Milky, whitish sap is particularly characteristic of Euphorbioideae; in *Euphorbia phosphorea* this even becomes phosphorescent on exposure (Spix & Martius, 1828). Among Crotonoideae, although some genera have white latex (such as *Manihot* and *Hevea*, genera with articulated laticifers), many others, such as *Aleurites*, *Codiaeum*, and *Neoboutonia*, have a clear, often viscous, latex. Red latex occurs in occasional species of several genera, such as *Alphandia*, *Baloghia*, *Cocconerion*, *Croton*, *Endospermum*, and *Pausandra* (McPherson & Tirel, 1987; Roosmalen, 1985; Schaeffer, 1971).

---

[1] I thank the following for supplying fresh material: Director, Adelaide Botanic Garden, Australia; Director, National Botanic Gardens, Zimbabwe; Curator, Mount Coot-tha Botanic Gardens, Queensland, Australia; Director, Jardin Botánico National, La Habana, Cuba; K. Alvin, Imperial College, London (material of *Androstachys johnsonii*); D. C. Lees (material from Panama and Cameroon). I am also very grateful to T. Lawrence (Jodrell Laboratory), P. Burns (Thames Polytechnic), and S. Hewis (Hatfield Polytechnic) for technical assistance and discussion, C. J. Humphries (British Museum, Natural History) for comments on the manuscript, and R. M. Harley (Royal Botanic Gardens, Kew) and A. M. Giulietti (University of São Paulo) for help in the field.

[2] Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, U.K.

ANN. MISSOURI BOT. GARD. 81: 270–282. 1994.

There are also records of latex in Acalyphoideae: species of *Omphalea* exude a clear or slightly milky latex, which oxidizes to red; *Macaranga* has latex ranging from clear to yellow, orange, or red (McPherson & Tirel, 1987).

Apart from a few scanty records in Acalyphoideae, laticifers are documented only in subfamilies Euphorbioideae and Crotonoideae (Rudall, 1987). Two laticifer types occur in Euphorbiaceae—articulated (chains of fused cells; recorded in a few genera of Crotonoideae only, e.g., *Hevea*) and nonarticulated (individual cells with intrusive growth, e.g., in *Euphorbia*, and many other genera). Some authors (e.g., Metcalfe, 1967) have regarded this as evidence of polyphyly. Indeed, Mahlberg et al. (1987) proposed that Euphorbiaceae should be regarded as three distinct families, one lacking laticifers, one with articulated laticifers, and one with nonarticulated laticifers, although most recent classifications (e.g., Webster, 1975) would reject this on the basis of other characters.

Materials and Methods

Material was obtained from various sources (Table 1). Herbarium material (dried leaves) was from the herbarium of the Royal Botanic Gardens, Kew (K). Leaves (L), stems (S), and in some cases, apices, fixed in formalin acetic alcohol (FAA), were acquired from the author's own collections in Brazil, living collections at Kew (HK), Limbe Botanic Garden, Cameroon, and the Smithsonian Tropical Research Institute (STRI), Panama. Seeds for embryo examination (E) were obtained from the Kew spirit collection (SC), Kew living collections (HK), other botanic gardens, and the author's own collections in Brazil. In many instances apparently sound seeds were found to lack embryos, or the embryos were not sufficiently well preserved for inclusion in this survey.

Fresh material was fixed in FAA for at least 48 hours, then stored in 70% alcohol. Herbarium material was revived by boiling in water. Leaves and stems were sectioned using a Reichert sliding microtome. Embryos and apices were embedded in Paraplast using standard methods of wax embedding, and sectioned using a Reichert rotary microtome. Sections were stained in safranin and Alcian blue, dehydrated through an alcohol series, and mounted in Euparal. Leaf fragments of *Codiaeum variegatum* were macerated by transferring them to a flask containing a mixture of equal parts of glacial acetic acid and 20-volume hydrogen peroxide, heating the mixture on a water bath for about 8 hours, then shaking it vigorously to achieve cell separation.

Observations

EMBRYOS

The distribution of nonarticulated laticifer initials in the Crotonoideae embryos examined here (excluding *Hevea confusa*) corresponds to the classical concept of initiation of nonarticulated laticifers (Schmalhausen, 1877), and is broadly consistent with records of development in *Euphorbia* and other Euphorbioideae, and indeed for nonarticulated laticifers in other dicotyledon families. Nonarticulated laticifer initials are present in the pericyclic region of the embryonic cotyledonary node, at a variable number of points around the axis. They subsequently permeate throughout other tissues by rapid intrusive growth, as Mahlberg & Sabharwal (1968) demonstrated in *Euphorbia*. Among different species of *Euphorbia* the number of initials varies from 4 or 8 to 12 or more (Chauveaud, 1891), the variation probably relating to differences in embryo size and number of primary vascular bundles in the different species. In mature embryos observed here the pericyclic ring consists of only ca. 8 initials in *Synadenium grantii* (Euphorbioideae) (Figs. 5, 6), but generally more in Crotonoideae: e.g., ca. 24 initials in *Baloghia lucida* (Fig. 2), *Croton megalobotrys*, *C. sylvaticus*, and a much larger number in *Aleurites triloba* (Fig. 8), although these may have proliferated by this stage. Furthermore, in Crotonoideae the initials occur toward the outer edge of the procambial tissue (i.e., within the protophloem region), contrary to the situation in Euphorbioideae (e.g., *S. grantii*, Figs. 5, 6), where they originate on the outside edge of the provascular tissue, as Mahlberg & Sabharwal (1968) also noted in *Euphorbia*. Initials elongate and branch intrusively, forming a complex laticiferous network. In *Baloghia lucida* the initials are considerably larger than surrounding cells (Figs. 3, 4), indicating possible polyploidy, although there is no evidence for this. Branches of the initials extend to the subepidermal region of the embryonic axis and toward the radicle (Fig. 1), thus forming two separate laticiferous rings, as de Bary (1884) and Chauveaud (1891) also noted in *Euphorbia*. Two distinct concentric rings (Fig. 7) were seen here in the hypocotyls of species of both Euphorbioideae (*Euphorbia lathyris* and *Synadenium grantii*) and Crotonoideae (*Baloghia lucida*, *Croton* spp.). Further branches proliferate around the cotyledonary node, close to the apex, and extend upwards into the cotyledons.

Mature embryos of *Hevea confusa* have a very short hypocotyledonary stem and two large broad cotyledons (Fig. 9). Typical articulated laticifers

TABLE 1. Taxa and material examined, with observations on laticifers and sclereids.

Taxon	Source & data[a]	Plant part[b]	Laticifers[c]	Sclereids in leaves[c]
Acalyphoideae				
Omphalea diandra L.	cult. STRI, Panama	LS	+ nonarticulated	–
Omphalea triandra L.	cult. STRI, Panama	LS	+ nonarticulated	–
Omphalea oleifera Hemsl.	cult. STRI, Panama	LS	+ nonarticulated	–
Mallotus subulatus Muell. Arg.	Limbe B.G., Cameroon	L	–	+
Crotonoideae				
Adenocline acuta Baill.	K: Muller & Scheepers 47	L	+ nonarticulated	–
Aleurites triloba J. R. Forster & G. Forster	HK: Hyland 2696	LS, E	+ nonarticulated	–
Baloghia lucida Endl.	Adelaide B.G., Australia	LS, E	+ nonarticulated	–
Bertya mitchellii (Sond.) Muell. Arg.	K: Sharrad 779	L	+ nonarticulated	–
Beyeria leschenaultii (DC.) Baill.	K: Rohrlach 408	L	+ nonarticulated	–
Codiaeum variegatum (L.) A. Juss.	HK (no data)	LS	+ nonarticulated	+ (older leaves)
Croton antisyphiliticus Mart. ex Muell. Arg.	Brazil: Harley et al. 25010 (K)	LS	+ nonarticulated	–
Croton comosus Muell. Arg.	Brazil: Harley et al. 25109 (K)	LS	+ nonarticulated	–
Croton conduplicatus Kunth.	Brazil: Harley et al. 25156 (K)	LS	+ nonarticulated	–
Croton heteropleurus Urb.	cult. Cuba B.G.	LS	+ nonarticulated	–
Croton megalobotrys Muell. Arg.	Z: Muller 818	LS, E	+ nonarticulated	–
Croton occidentalis Muell. Arg.	Brazil: Harley et al. 24827 (K)	LS	+ nonarticulated	–
Croton sagreanus Muell. Arg.	cult. Cuba B.G.	LS	+ nonarticulated	–
Croton sylvaticus Hochst.	Z: Ritchken s.n.	LS, E	+ nonarticulated	–
Croton sp.	Brazil: Harley et al. 24832 (K)	LS	+ nonarticulated	–
Croton sp.	Brazil: Harley et al. 25091 (K)	LS	+ nonarticulated	–
Croton sp.	Brazil: Harley et al. 25226 (K)	LS, E	+ nonarticulated	–
Croton sp.	Brazil: Harley et al. 24986 (K)	LS	+ nonarticulated	–
Cyrtogonone argentea Prain	K: Thomas 4738	L	+ nonarticulated (stem only)	+

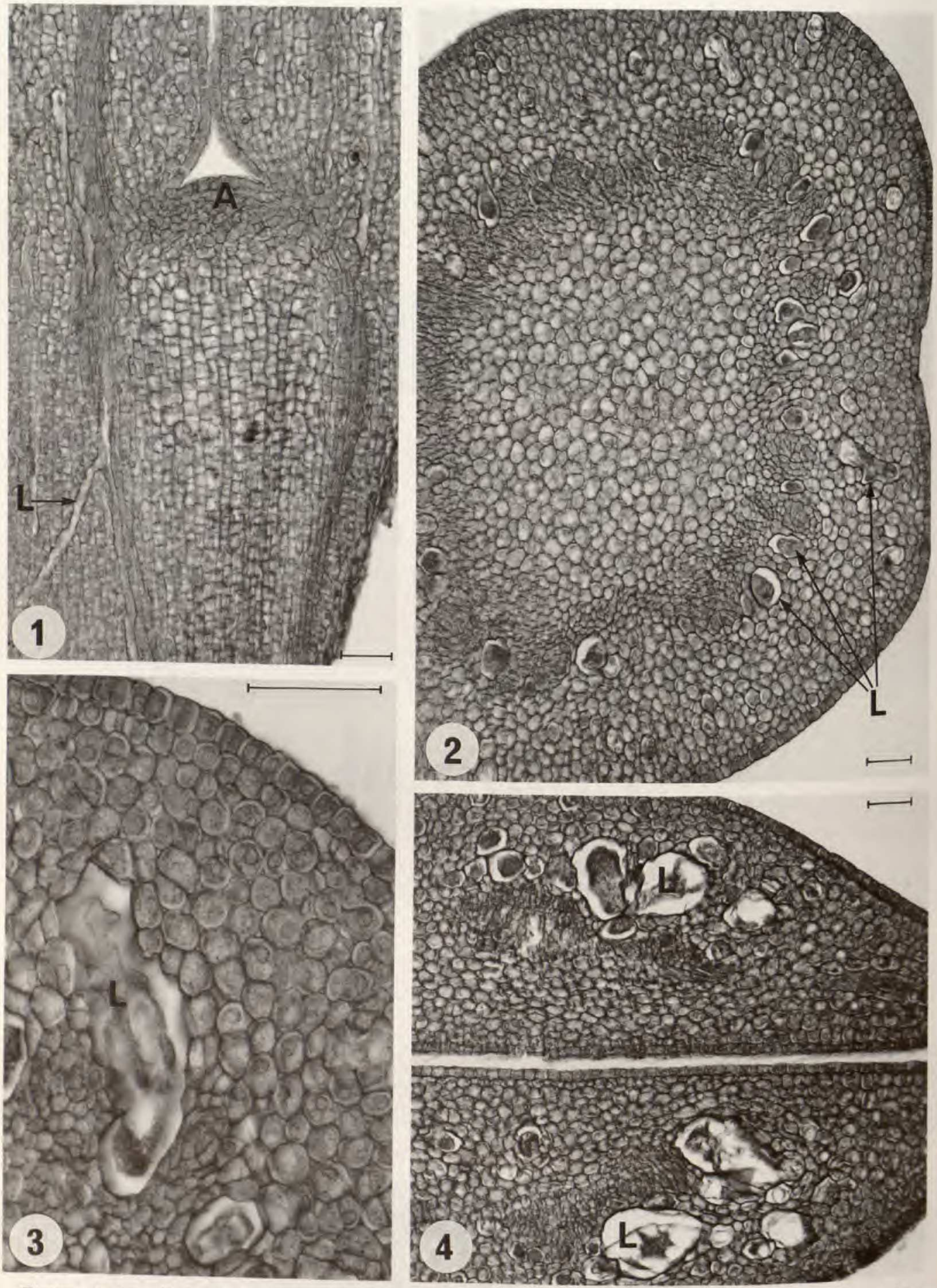
TABLE 1. Continued.

Taxon	Source & data[a]	Plant part[b]	Laticifers[c]	Sclereids in leaves[c]
Garcia nutans Rohr	K: Gillis 15070	L	+ nonarticulated	–
Grossera vegenei Pax	K: Bamps 2363	L	–	+
Hevea confusa Hemsl.	SC: cult. Castleton Gdns.	E	+ articulated	–
Jatropha curcas L.	HK (no data)	LS, E	+ nonarticulated	–
Manihot sp. aff. *caerulescens* Pohl.	Brazil: Harley et al. 25098 (K)	LS	+ articulated	–
Micrandra elata Muell. Arg.	K: Lindeman et al. 256	L	+ nonarticulated	–
Micrandra minor Benth.	K: Schultes & Lopez 8959	L	+ nonarticulated	–
Micrandra siphonoides Benth.	K: Schultes & Lopez 10180	L	+ nonarticulated	–
Micrandra prucei (Muell. Arg.) Schultes	K: Schultes & Pires 9057	L	+ nonarticulated	–
Neoboutonia macrocalyx Pax	K: Lewalle 8000	L	+ nonarticulated	–
Pausandra macropetala Ducke	K: Ducke 7148	L	+ nonarticulated (petiole only)	+
Ricinocarpus ledifolius F. Muell.	K: Coveney 6842	L	+ nonarticulated	
Ricinocarpus pinifolius Desf.	K: Coveney 7253	L	+ nonarticulated	
Ricinodendron heudolotii (Baill.) Pierre ex Hecke	K: Troupin 3450	L	+ nonarticulated	–
Spirostachys venenifera (Pax) Pax	K: Kisena 342	L	+ nonarticulated	–
Trigonostemon chinensis Merrill	K: Thow 78487	L	–	+
Vernicia cordata (Thunb.) Airy Shaw	K: s.n. (cult. Grossens)	L	+ nonarticulated	–
Euphorbioideae				
Euphorbia lathyris L.	HK: Aronson s.n.	E	+ nonarticulated	–
Synadenium grantii Hook.	HK: Brandham et al. 2549	E	+ nonarticulated	–

[a] STRI = Smithsonian Tropical Research Institute; B.G. = Botanic Garden; K = herbarium of the Royal Botanic Gardens, Kew; HK = living collections at Kew; Z = herbarium of the Institut für Systematische Botanik, Zürich; SC = Kew spirit collection.

[b] E = seeds for embryo extraction; L = leaves; S = stems.

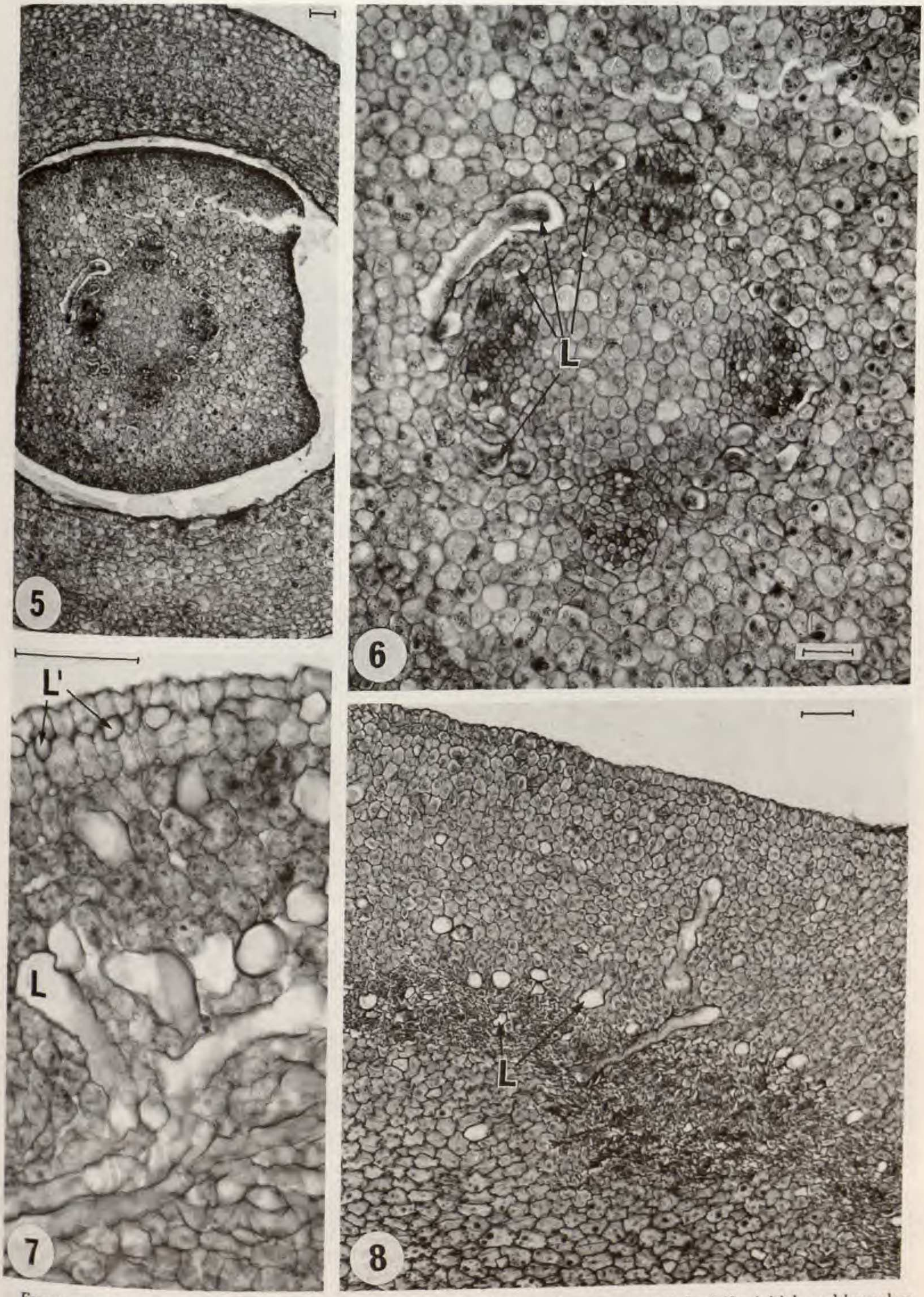
[c] + = present; – = absent.



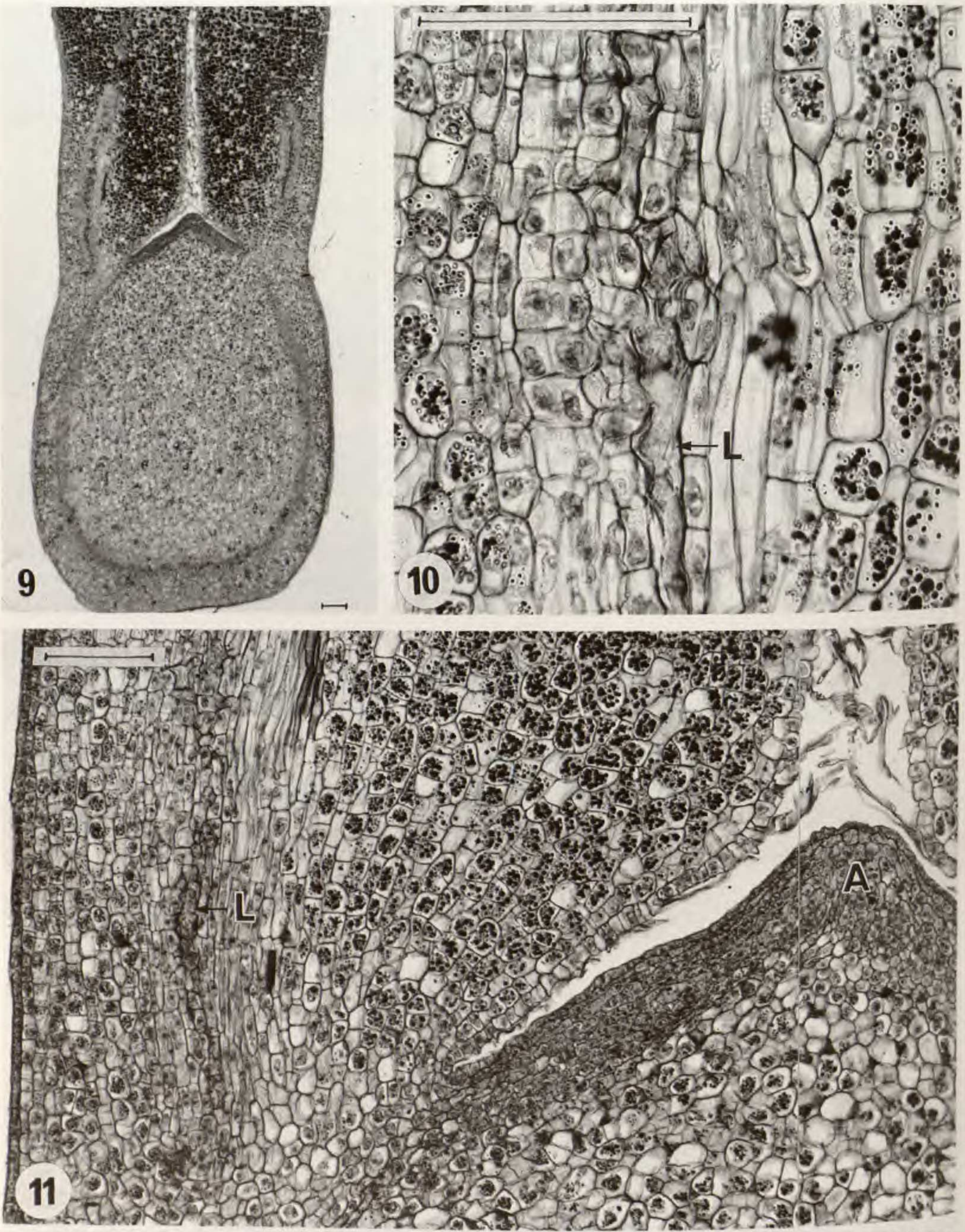
FIGURES 1–4.[3] Embryos of *Baloghia lucida*. — 1. Longitudinal section through apex (A). Laticifer (L) branching toward subepidermal ring. — 2. Cross section through hypocotyl, with laticifers (L) toward periphery of vascular tissue. — 3. Detail of cross section through hypocotyl. — 4. Cross section of cotyledons. L = laticifer. Scale bars = 50 μm.

---

[3] Voucher or source information is in Table 1, unless given in the caption.



FIGURES 5–8.[3] Cross sections of embryo hypocotyls.—5, 6. *Synadenium grantii.* Laticifer initials and branches (L) around outer edge of vascular tissue. Generally a single initial is present on each side of each of four vascular bundles, forming ca. eight initials, which then ramify.—7. *Euphorbia latifolia.* Distinct subepidermal ring of laticifers (L') and inner ramifying laticifers (L).—8. *Aleurites triloba.* Laticifer initials (L) in vascular tissue. Scale bars = 50 μm.



FIGURES 9–11.[3] Longitudinal sections of *Hevea confusa* embryos.—9. Short hypocotyl and broad cotyledons.—10. Articulated laticifers (L).—11. Region near apex (A), showing laticifers (L) in cotyledon. Scale bars = 100 μm.

(Fig. 10) are present in the outer part of the provascular tissue (i.e., the protophloem region, as with nonarticulated laticifers of other genera) of the cotyledonary node and in the base of the cotyledons (Fig. 11). The cotyledonary initials are the most well developed at this stage, as Scott (1886) also found in *Hevea brasiliensis*. Intrusive growth is not pronounced, although some short branches are present. Later articulated laticifers form elongated intrusive branches between surrounding cells in the same way as nonarticulated laticifers, especially in the leaf mesophyll (Rudall, 1987).

LEAVES AND STEMS

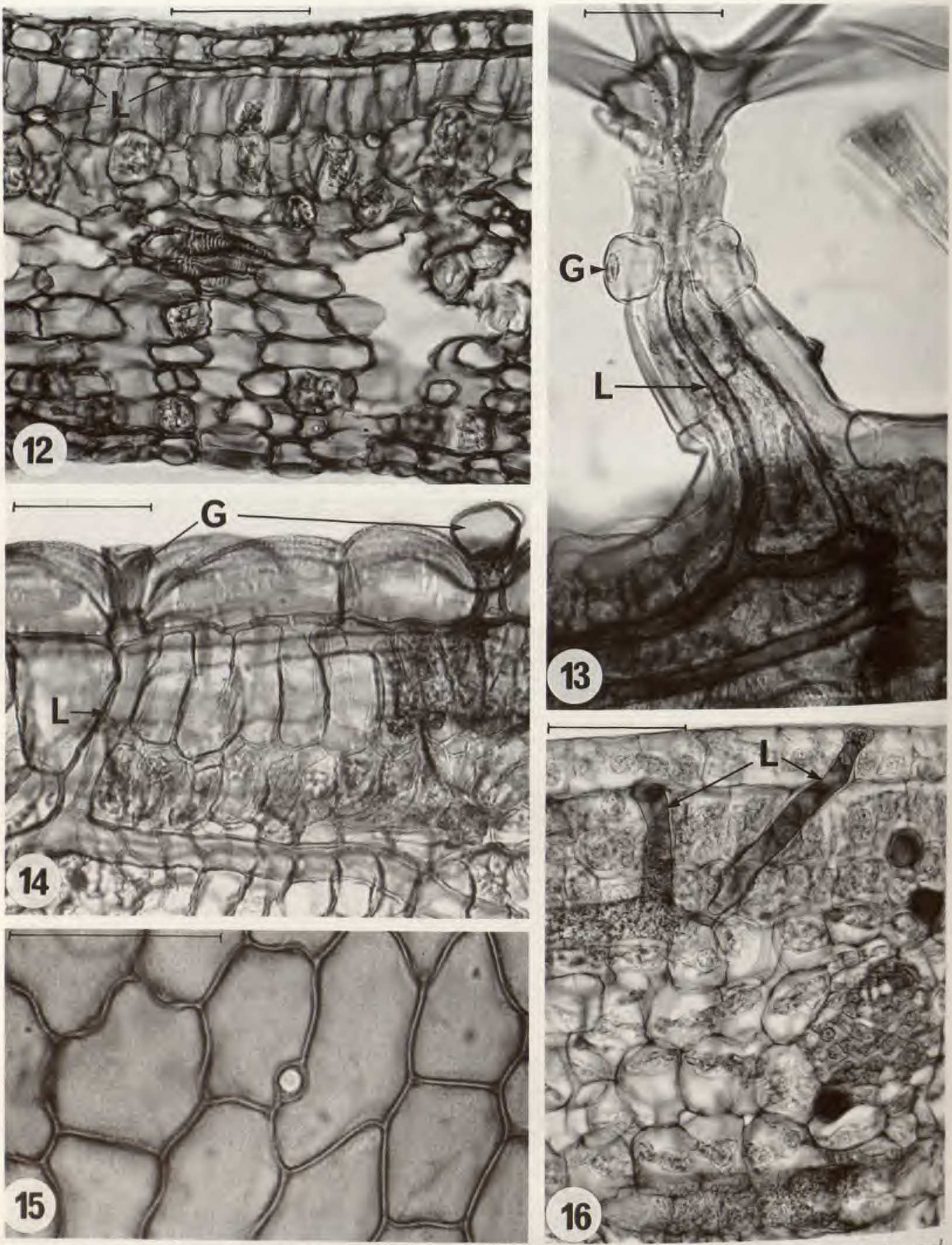
Acalyphoideae. *Omphalea*, which exudes a clear latex that becomes red on oxidation, has abundant nonarticulated laticifers in the leaf mesophyll and stem. Laticifers were also observed in the tissue above extra-floral nectaries on the abaxial leaf surface. In *Mallotus subulatus*, although laticifers are absent in mature leaves, many narrow intrusive thick-walled sclereid branches are present.

Crotonoideae. Thin-walled laticifers were observed here in most Crotonoideae examined (Table 1): *Adenocline acuta, Baloghia lucida, Bertya mitchellii, Beyeria leschenaultii, Codiaeum variegatum* (Figs. 15, 16), *Croton* spp. (Figs. 13, 17–19), *Cyrtogonone argentea* (stem only), *Garcia nutans* (Fig. 12), *Jatropha curcas* (Fig. 20), *Micrandra* spp., *Neoboutonia macrocalyx*, *Pausandra macropetala* (petiole only), *Ricinodendron heudelotii*, *Spirostachys venenifera*, and *Vernicia caudata*. Thick-walled sclereids were observed in leaves of *Grossera veginei* and *Trigonostemon chinensis* (Fig. 22) (in the latter sometimes protruding between epidermal cells or to hair bases). Pax (1884) recorded laticifers in *Trigonostemon*; furthermore, in our material of *Cyrtogonone argentea*, laticifers are present in the stem phloem, cortex, and pith, but only thick-walled sclereids in the leaves, indicating that the "sclereids" in these cases may be thick-walled laticifers. Similarly, in *Pausandra macropetala* laticifers were observed in the petiole, but only thick-walled sclereids in the mesophyll. In *Codiaeum variegatum*, sclereids were present in older leaves, but absent in younger, as Rao & Tewari (1960) also reported. In *Codiaeum variegatum*, where laticifers frequently intrude between epidermal cells, as in *Baloghia lucida* (Rudall, 1987), the fact that laticifers are continuously growing is demonstrated by the presence of many more points of laticifer intrusion in epidermises of older leaves than young leaves (Figs. 15, 16). In some species latex is recorded only in young tissues (e.g., in *Glycydendron*, Roosmalen, 1985), and laticifers presumably cease to function (probably becoming thick-walled; see below). The distinction between the two cell types in these taxa is therefore not always clear; "laticifers" in young leaves may become "sclereids" in older ones. In the literature such cells (with intrusive branches) are termed laticifers if they are thin-walled, and sclereids if they are thick-walled.

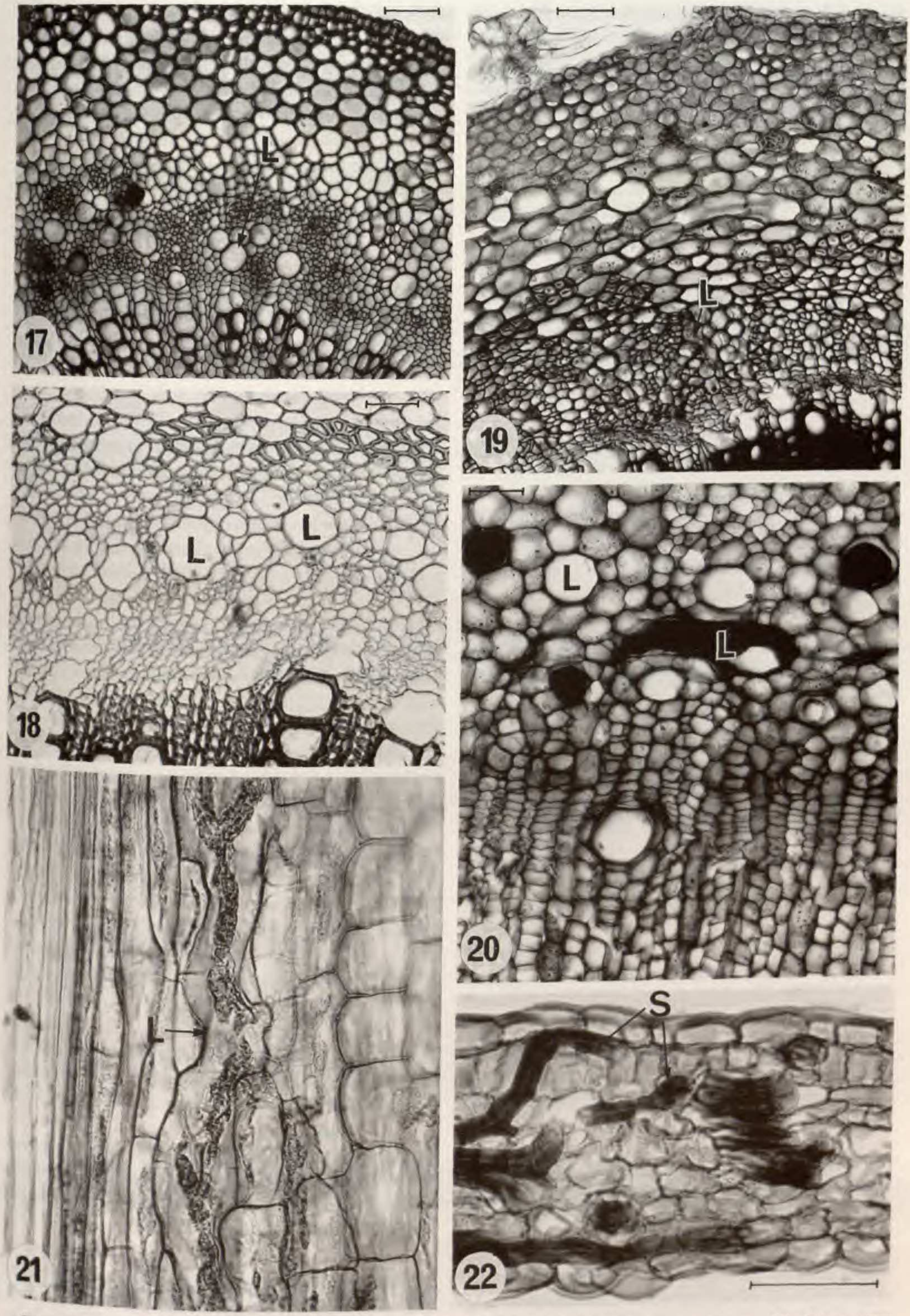
Occasional cross-walls were observed in leaf laticifers of *Micrandra elata*, as other workers have also occasionally reported in other genera (e.g., de Bary, 1884, in *Euphorbia lathyris*; Dehgan & Craig, 1978, in *Jatropha* spp.). Otherwise laticifer structure is essentially similar in all genera concerned (apart from the articulated forms occurring in *Hevea*, *Manihot*, and *Cnidoscolus*), the main differences being in size and quantity. In Crotonoideae laticifers generally occur in the phloem of the stem, petiole, and midrib bundles, and may be large and easily distinguishable in cross section (Fig. 18), or sometimes smaller (Fig. 19). Laticifers in the leaf mesophyll range in size from narrow (Fig. 12) to broader than neighboring mesophyll cells. In several species laticifers extend either directly to the plant surface (e.g., in *Codiaeum variegatum*, Figs. 15, 16) or into the bases of trichomes (e.g., *Croton* spp., Fig. 13). In *Beyeria* and *Ricinocarpus*, laticifers were occasionally observed in direct contact with small glandular hairs on the plant surface (Fig. 14). In many cases (e.g., *Codiaeum variegatum*), the narrowest laticifers, immediately within the epidermis, are the most highly branched.

A wide variation of nonarticulated laticifers is displayed by various species of *Croton*. Most species have abundant nonarticulated laticifers, though sometimes less frequent in older stems (e.g., in *C. comosus*). Distribution ranges from extremely abundant and highly branched in all aerial tissues (e.g., *C. conduplicatus*, Fig. 19) to (rarely) apparently absent. Other authors, such as McPherson & Tirel (1987), have reported latex apparently absent in some species of *Croton*, and this variation may well have some taxonomic significance within the genus. However, species that lack laticifers may have the capacity to develop them under certain environmental conditions, or at particular stages in their life cycle, and a better understanding of the function of latex in different species would be necessary to establish this.

In this investigation, typical articulated laticifers were observed in stems of *Manihot* sp. aff. *caerulescens* (Fig. 21) and *Hevea confusa* embryos (Figs. 9–11). In *Manihot*, *Hevea*, and *Cnidoscolus*, which have articulated laticifers in the stems, transitional nonarticulated (intrusively branched) forms are also present, particularly in the leaves (Rudall, 1987). Articulated laticifers (recorded in *Hevea*, *Manihot*, and *Cnidoscolus*: Rudall, 1987) are continuously produced in the developing primary phloem, and also in the vascular cambium. However, in *Croton conduplicatus* occasional (rare) instances were observed of ray initials in the vascular cambium intruding between adjacent phloem ray cells in the manner of young laticifer initials (Rudall, 1989), i.e., new laticifer initials forming in the vascular cambium. Since no evidence of cell fusion was



FIGURES 12–16.[3] Laticifers (L) in leaves.—12. *Garcia nutans*, cross section.—13. *Croton* sp. (*Harley et al. 24986*), laticifers branching into base of stellate hair, with glandular region (G).—14. *Beyeria leschenaultii*, cross section. Laticifers extending to bases of glandular hairs (G). 15, 16. *Codiaeum variegatum*.—15. Leaf surface, showing point of intrusion of laticifer between epidermal cells.—16. Cross section, with laticifers intruding between epidermal cells. Scale bars = 50 μm.



FIGURES 17–22.[3] 17, 18. *Croton* sp. (*Harley et al. 24843*).—17. Midrib, cross section.—18. Stem, cross section.—19. *Croton conduplicatus*, stem cross section.—20. *Jatropha curcas*, stem cross section.—21. *Manihot* sp., longitudinal section of stem, phloem region, showing laticifer.—22. *Trigonostemon chinensis*, leaf cross section, showing sclereids (S). Scale bars = 50 μm. L = laticifer.

found, these are nonarticulated laticifers. This species is unusual in the abundance of its laticifers and their degree of branching, and it is therefore possible that this apparently very unusual phenomenon is simply more detectable in this material, because new laticifers produced in the vascular cambium begin to branch immediately, rather than elongating for a period. A "secondary" laticifer (formed from the vascular cambium) that elongated in the region close to the vascular cambium would be virtually indistinguishable from a "primary" laticifer (formed in primary tissues) that extended into this region from the cortex; indeed many species have abundant laticifers in the most recently formed secondary phloem, and their origin is difficult to determine.

DISCUSSION

LATICIFER EVOLUTION

The traditional difference between the articulated and nonarticulated types of laticifer is that the former are multicellular and the latter unicellular. Typical articulated laticifers are often easily recognizable by their eccentrically convoluted appearance (Fig. 21). Nevertheless, as de Bary (1884) and other early workers have also observed, there are several similarities and transitional forms that tend to narrow the gap between the extremes of both categories: (1) In Crotonoideae nonarticulated laticifers originate in the protophloem of the embryo, and (as Gaucher, 1902, also noted) in general predominate in the phloem of older tissues, in common with articulated laticifers of other crotonoid genera, and in contrast to the condition of Euphorbioideae. (2) Single cell members of articulated laticifers in leaves of, e.g., *Hevea* grow intrusively between mesophyll cells, in the same manner as nonarticulated laticifers (Rudall, 1987). Boblioff (1923) observed these intrusive "amoeboid" forms both in leaves and the inner integument of the seed of *Hevea*. Other anomalous cell types have also been reported by several early workers; for example, Pax mentioned that in *Joannesia*, *Garcia*, and *Aleurites* (all Crotonoideae), certain "closed sacs" grow to a great length. The "articulated laticifers" that Dehgan & Craig (1978) described in *Jatropha* are very different from those of *Hevea*, *Cnidoscolus*, and *Manihot*, but may represent another form. (3) Nonarticulated (i.e., intrusive, unicellular) laticifers, although normally primary in origin, have also been observed in *Croton* to originate in secondary tissue derived from the vascular cambium (Rudall, 1989), a type of development usually associated only with articulated laticifers.

Scott (1886) believed, following Pax (1884), that articulated and nonarticulated laticifers evolved separately, both from secretory sacs; in fact, rows of large parenchymatous cells with dark contents frequently occur in the phloem of species without latex, such as *Androstachys johnsonii* and *Mallotus subulatus*. Furthermore, occasional cross-walls have been reported in nonarticulated laticifers of several species, such as *Micrandra elata*. However, an alternative theory, probably more plausible in view of the similarities demonstrated here between the two laticifer types, is that articulated laticifers of *Hevea*, *Cnidoscolus*, and *Manihot*, and the transitional forms of other genera represent more recent developments from the nonarticulated type (although further data are essential, particularly on laticifer ontogeny). The nonarticulated type is by far the most common type among Euphorbiaceae, and indeed other dicotyledons, and is therefore probably the plesiomorphic type in this family.

LATICIFERS AND SCLEREIDS

Elongated "fiberlike," occasionally branched sclereids occur in mesophyll of leaves of many euphorbiaceous genera, generally (though not exclusively) where laticifers are absent. In view of the apparent relationship between the two cell types (see below and Observations, above), this near-exclusivity is consistent with a probable homology between them, although this hypothesis requires further testing. Metcalfe & Chalk (1950) and Rao & Das (1979) recorded sclereids in several genera, especially among Acalyphoideae, such as *Acalypha* and *Chaetocarpus*. *Androstachys johnsonii* (Oldfieldioideae), which lacks latex, has copious highly branched gelatinous sclereids in the mature leaves, similar to laticifers in many respects, associated with the epidermis and veins, and often also with the bases of probable water-absorbing trichomes (Alvin, 1987). Among Crotonoideae, several genera (e.g., *Grossera*, *Pausandra*, and *Trigonostemon*) have sclereids instead of laticifers in the leaves, although stems have not been investigated in these cases: *Cyrtogonone argentea* has thin-walled laticifers in the stem, but only sclereids in the leaves. In all cases the sclereids resemble laticifers in structure and distribution, both cell types being extremely elongated and associated with vascular tissue and epidermis; they are not easily distinguishable in sections, except in terms of wall thickness. Moreover, thick-walled laticifers are not uncommon (e.g., in stems of *Euphorbia abdelkuri*; Rudall, 1987). Rao & Tewari (1960) reported that in *Codiaeum variegatum*, laticifers in young leaves actually become sclereids in older leaves; indeed in our material of this species sclereids were present in older leaves, and absent in younger.

SYSTEMATIC AND PHYLOGENETIC CONSIDERATIONS

Many plants are known to produce latex, but the capacity for latex production does not in itself necessarily imply relationship. Latex-producing dicotyledon families, such as Apocynaceae, Asclepiadaceae, Eucommiaceae, Sapotaceae, and Moraceae, are widely distributed throughout various dicotyledon orders. Nevertheless, as many authors (e.g., Mahlberg & Sabharwal, 1968) have also observed, there is remarkable similarity in laticifer morphology and development between comparatively unrelated dicotyledons, especially considering the anomalous nature of the cell types concerned. The apparent relationship between laticifers and branched sclereids (astrosclereids) is not restricted to Euphorbiaceae; in other families the two cell types are often mutually exclusive in related genera, also indicative of a possible homology between them. A survey of dicotyledon families in this respect, though inappropriate here, might shed further light on the subject and help to indicate affinities of Euphorbiaceae. Sister-group relationships of Euphorbiaceae have been much disputed, but probably exist among the Malvales, Geraniales, or Linales (Webster, 1987a, b). Although sclereids occur widely among these orders, there are very few latex-producing families; therefore, in the absence of a latex-producing sister group, and if Euphorbiaceae is indeed monophyletic, the most likely inference is that latex production evolved de novo within the family.

Within Euphorbiaceae, Webster (1987b) postulated that Crotonoideae and Euphorbioideae (latex and laticifers usually present) evolved independently from Acalyphoideae (latex and laticifers rarely present). Subfamilies Oldfieldioideae and Phyllanthoideae (latex and laticifers absent) are closely linked to each other. Thus there are three main divisions within Euphorbiaceae on the basis of latex and other characters: Oldfieldioideae/Phyllanthoideae, Acalyphoideae, and Crotonoideae/Euphorbioideae. However, Acalyphoideae divides into two groups: without latex (most genera) and with latex (e.g., *Macaranga*, *Omphalea*). If (as seems most likely) latex production evolved within Euphorbiaceae (in the Euphorbioideae/Crotonoideae lineage), the abundant presence of laticifers in *Omphalea* casts doubt on its systematic position in Acalyphoideae. Variation in this character in Acalyphoideae (also in a few Crotonoideae) indicates paraphyly, although it is also possible that a reversal (i.e., loss of latex) may yet be demonstrated on the basis of congruence in other characters.

LITERATURE CITED

ALVIN, K. L. 1987. Leaf anatomy of *Androstachys johnsonii* Prain and its functional significance. Ann. Bot. 59: 579–591.

BARY, A. DE. 1884. Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns. [English translation.] Clarendon Press, Oxford.

BOBLIOFF, W. 1923. Anatomy of *Hevea brasiliensis*. Zurich.

CHAUVEAUD, M. L. G. 1891. Recherches embryogéniques sur l'appareil laticifère des Euphorbiacées, Urticacées, Apocynées et Asclépiadées. Ann. Sci. Nat., Botanique 14(1–2): 1–160.

DEHGAN, B. & M. E. CRAIG. 1978. Types of laticifers and crystals in *Jatropha* and their taxonomic implications. Amer. J. Bot. 65: 435–352.

GAUCHER, L. 1902. Recherches anatomiques sur les Euphorbiacées. Ann. Sci. Nat., Botanique 15(1): 161–309.

MAHLBERG, P. G. & P. S. SABHARWAL. 1968. Origin and early development of non-articulated laticifers in embryos of *Euphorbia marginata*. Amer. J. Bot. 55: 375–381.

———, D. G. DAVIS, D. S. GALITZ & G. D. MANNERS. 1987. Laticifers and the classification of *Euphorbia*: The chemotaxonomy of *Euphorbia esula* L. Bot. J. Linn. Soc. 94: 165–180.

MCPHERSON, G. & C. TIREL. 1987. Flore de la Nouvelle Calédonie et dépendences. Euphorbiaceae I. Mus. d'Hist. Nat., Paris.

METCALFE, C. R. 1967. Distribution of latex in the plant kingdom. Econ. Bot. 21: 115–127.

——— & L. CHALK. 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford.

PAX, F. 1884. Die Anatomie der Euphorbiaceae in ihrer Beziehung zum System Derselben. Bot. Jahrb. 5: 384–421.

RAO, A. R. & J. P. TEWARI. 1960. On the morphology and ontogeny of the foliar sclereids of *Codiaeum variegatum* Blume. Proc. Nat. Inst. Sci. India. 26B: 1–6.

RAO, A. T. & S. DAS. 1979. Leaf sclereids—Occurrence and distribution in the angiosperms. Bot. Not. 132: 319–324.

ROOSMALEN, M. G. M. VAN. 1985. Fruits of the Guianan Flora. Inst. Syst. Bot., Utrecht University.

RUDALL, P. J. 1987. Laticifers in Euphorbiaceae—A conspectus. Bot. J. Linn. Soc. 94: 143–163.

———. 1989. Laticifers in vascular cambium and wood of *Croton* spp. (Euphorbiaceae). IAWA Bull. n.s. 10: 379–383.

SCHAEFFER, J. 1971. A revision of *Endospermum* Benth. (Euphorbiaceae). Blumea 19: 171–192.

SCHMALHAUSEN, J. 1877. Beiträge zur Kenntnis das Milchsaftbehälter der Pflanzen. Mém. Acad. Imp. Sci. St. Petersburg. Ser. 7 24: 1–27.

SCOTT, D. H. 1884a. On the laticiferous tissue of *Manihot glaziovii* (the Ceara rubber). Quart. J. Microsp. Sci. 24: 193–203.